
TROPICAL WESTERN ATLANTIC SPECIES OF *DIAULULA* BERGH, 1878 (MOLLUSCA, NUDIBRANCHIA), WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT. The genus *Diaulula* is represented in the tropical western Atlantic by two species: *Diaulula greeleyi*, a trans-Panamanian species also reported from the Pacific coasts of Mexico and Costa Rica, and *Diaulula farmersi*, a new species from the Florida Keys. Differences in color and anatomy separate these two species as *D. farmersi* has a yellowish background color, a white gill, and the bursa copulatrix and prostate are proportionally smaller. Examination of specimens of different sizes of *D. greeleyi*, as well as a review of the literature from other geographic regions, reveals that this species shows little anatomical variability, supporting the separation of *D. farmersi*. Two further sympatric species that are superficially similar to *D. greeleyi*, *Discodoris mortenseni* and *Discodoris phoca*, differ from members of *Diaulula* in having jaws and in other anatomical features.

INTRODUCTION

The genus *Diaulula* was originally introduced by Bergh (1878) based on *Doris sandiegensis* Cooper, 1863, from California. The main characteristics defined by Bergh (1878) for this genus were the presence of a villous, silky dorsum, notched and grooved anterior border of the foot, tripinnate branchial leaves, absence of jaws, presence of a large prostate, and unarmed penis.

Subsequently, Bergh (1905, 1907) introduced four additional species of *Diaulula*: *Diaulula rubra* Bergh, 1905 (from the Philippines), *Diaulula gigantea* Bergh, 1905 (from Indonesia), *Diaulula capensis* Bergh, 1907, and *Diaulula morosa* Bergh, 1907, both from South Africa. The generic identity of all of these species is uncertain, except for *D. gigantea*, which, according to Valdés (2002), is a synonym of *Sebadoris nubilosa* (Pease, 1871). Eliot (1907) and Marcus (1959) transferred the South American species *Doris vestita* Abraham, 1877, and *Doris hispida* d'Orbigny, 1837, respectively, to *Diaulula*. Because of the uncertain placement of the tropical Indo-Pacific and South African species, the genus *Diaulula* was thought to be restricted to cold waters in North and South America.

Thompson (1975) and McDonald (1983) regarded *Diaulula* as a synonym of *Discodoris*, based on the similar size, shape, mode of life, radula, and reproductive organs of both genera. Behrens (1991) did not agree with that synonymy and maintained the usage of *Diaulula* as a valid genus for *Diaulula sandiegensis*.

Valdés and Gosliner (2001) reconstructed the phylogenetic relationships of the caryophyllidia-

bearing dorids, which, according to these authors, are a monophyletic group. Valdés and Gosliner (2001) restricted the use of the name *Diaulula* to species with elongate caryophyllidia, a large prostate with two differentiated portions, penis and vagina unarmed, labial cuticle smooth, and radular teeth hamate and smooth. Additionally, anatomical examination of specimens of *Doris punctuolata* d'Orbigny, 1837 (the type species of *Anisodoris* Bergh, 1898), revealed that it has the same features as members of *Diaulula*, so these two genus names were regarded as synonyms. This new classification implies that a number of species of caryophyllidia-bearing dorids that have been described in various genera probably belong to the genus *Diaulula*, which is probably a much larger clade than originally thought. For instance, following the new diagnosis of *Diaulula*, Camacho-García and Valdés (2003) transferred the tropical Atlantic species *Peltodoris greeleyi* MacFarland, 1909 to *Diaulula*, and at the same time synonymized the tropical eastern Pacific species *Peltodoris nayarita* Ortea and Llera, 1981 with it. They also transferred the Panamic species *Discodoris aurila* Ev. Marcus, 1976 to *Diaulula*. Additionally, Valdés and Muniain (2002) regarded *Diaulula vestita* as a probable synonym of *Diaulula punctuolata*.

Recent fieldwork in the Florida Keys revealed the presence of an additional species of the genus *Diaulula* in the Caribbean. The present paper deals with this species and provides up-to-date descriptions and classifications for western Atlantic species of *Diaulula*.

MATERIAL AND METHODS

The material examined is deposited at the Natural History Museum of Los Angeles County (LACM). Specimens were dissected by making a dorsal incision. The internal fea-

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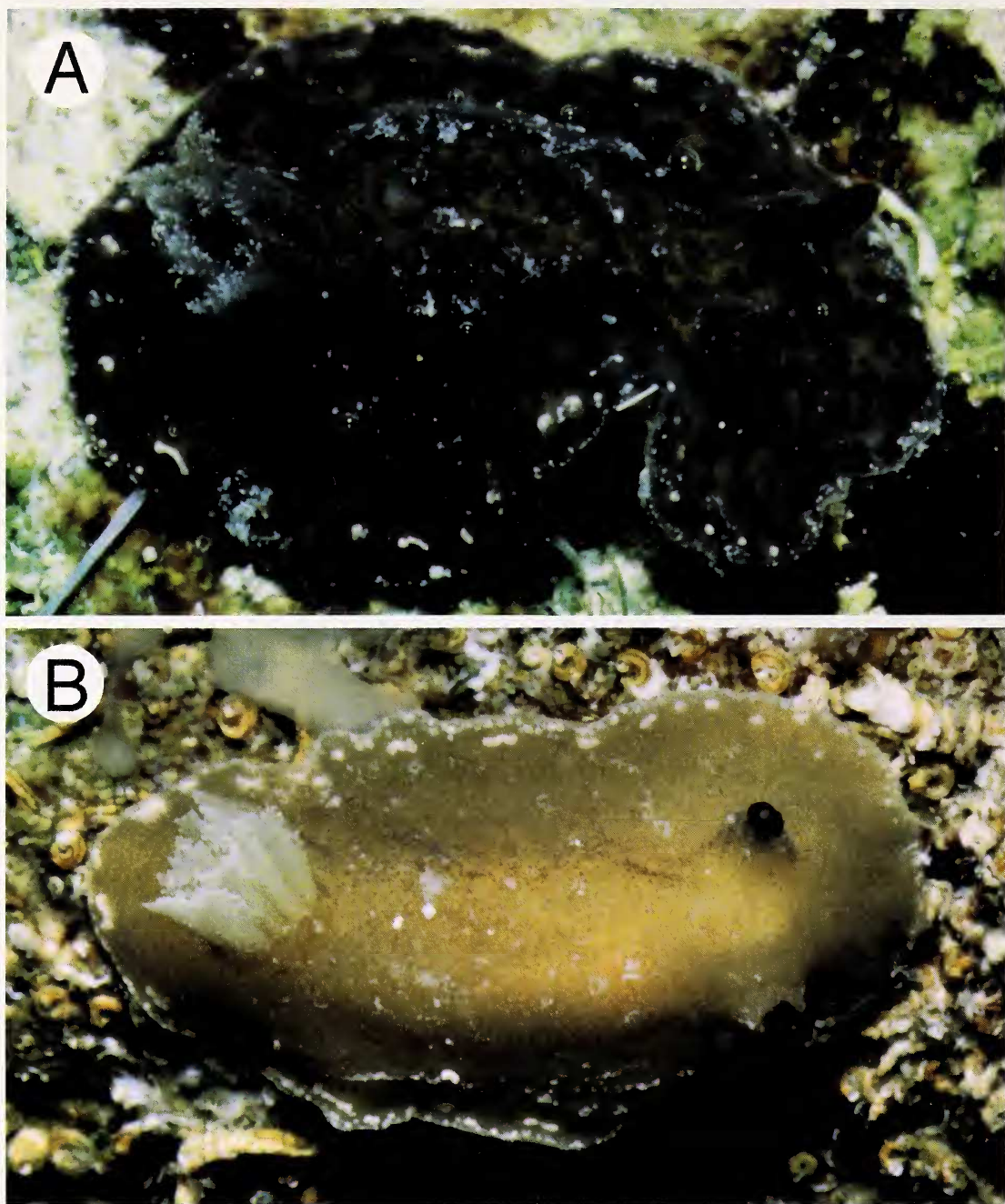


Figure 1 Living animals: A, *Diaulula greeleyi* (MacFarland, 1909), Key Largo, Florida, (LACM 2003-41.4). B, *Diaulula farmersi* n. sp., holotype, Key Largo, Florida, (LACM 3016)

tures were examined and drawn using a dissecting microscope with a *camera lucida*. A portion of the mantle was critical point dried for the Scanning Electron Microscope (SEM). The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination with the SEM. Features of living animals were recorded from field photographs and notes.

SPECIES DESCRIPTIONS

Discodorididae Bergh, 1891

Diaulula Bergh, 1880

Diaulula greeleyi (MacFarland, 1909)

Figs. 1A, 2-3

Peltodoris greeleyi MacFarland, 1909:84-88, pl.

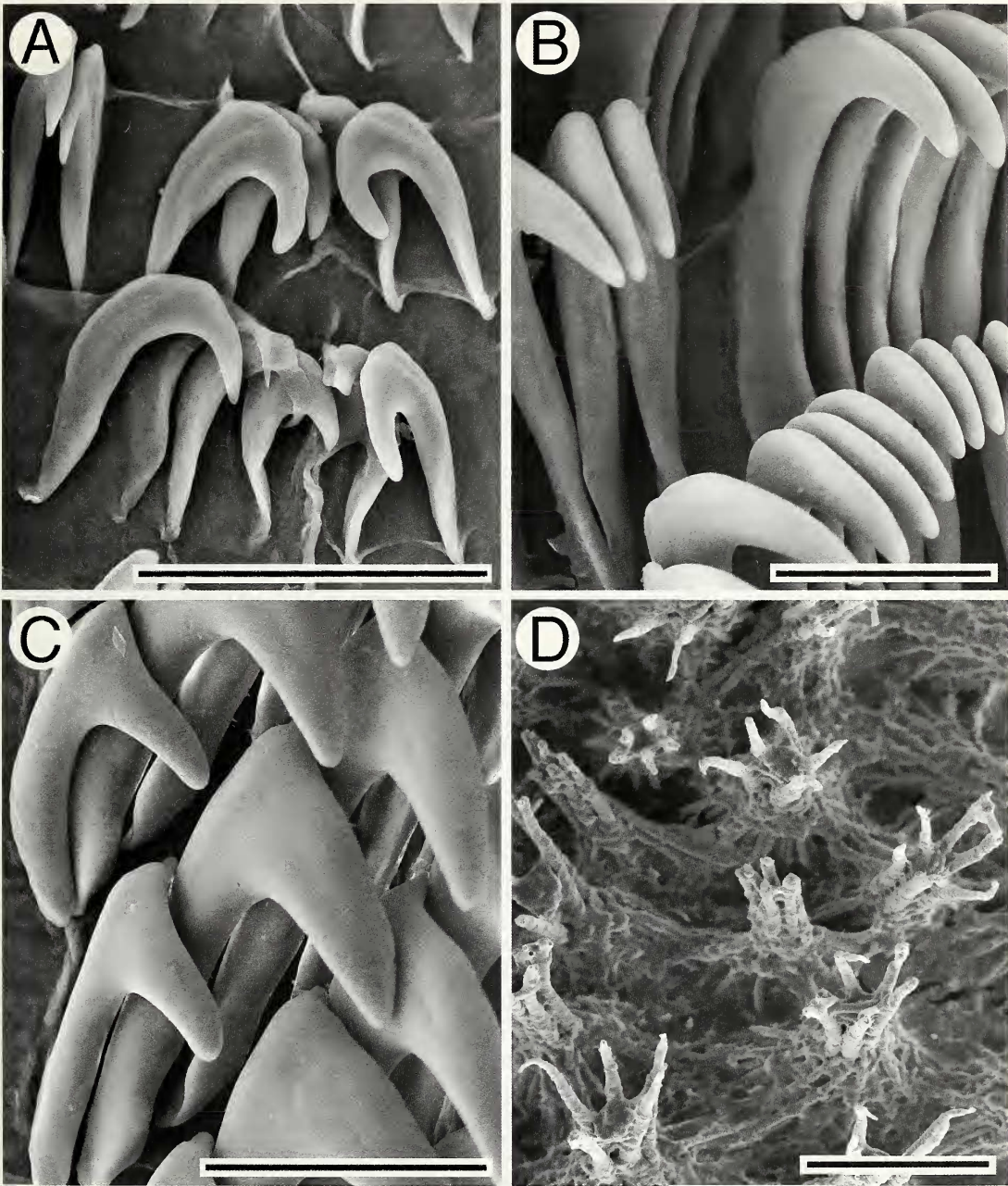


Figure 2 *Diaulula greeleyi* (MacFarland, 1909), Key Largo, Florida, (LACM 2003-41.4), scanning electron micrographs of radula and dorsum: A, Innermost lateral teeth, scale bar = 50 μm . B, Midlateral teeth, scale bar = 30 μm . C, Outermost lateral teeth, scale bar = 50 μm . D, Caryophyllidia, scale bar = 100 μm

15, figs. 77–82; Marcus, 1955:137–140, pl. 14, figs. 126–132; Marcus and Marcus, 1967:72–74, text figs. 94–98; Eyster, 1980:588.
Peltodoris nayarita Ortea and Llera, 1981:47–51, text figs. 1–4 (also cited as *Anisodoris*); Bertsch et al., 2000:100.
Diaulula greeleyi (MacFarland): Camacho-García

and Valdés, 2003:71–75, text figs. 1C, 4A–D, 5A–D.
TYPE MATERIAL. Holotype. Alagoas, Riacho Doce, Brazil, 28 July 1899, 1 specimen, 9 mm preserved length, leg. A.W. Greeley (California Academy of Sciences 21021).

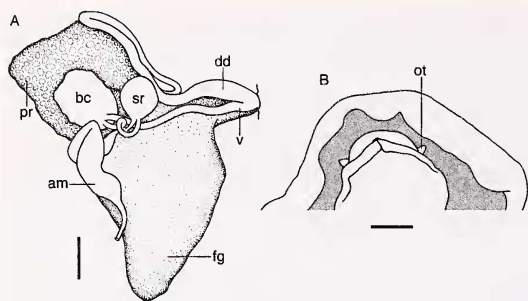


Figure 3 *Diaulula greeleyi* (MacFarland, 1909), Key Largo, Florida, (LACM 2003-41.4), anatomy: A, Reproductive system, scale bar = 500 μm . B, Ventral view of the mouth area, scale bar = 2 mm. Abbreviations: am = ampulla; bc = bursa copulatrix; dd = deferent duct; fg = female glands; ot = oral tentacle; pr = prostate; sr = seminal receptacle; v = vagina

MATERIAL EXAMINED. Shore in front of the Bayside Resort (mile marker 99.5), Key Largo, Monroe County, Florida, 13 July 2003, 1–2 m depth, 3 specimens, 5–13 mm preserved length, leg. A. Valdés (LACM 2003-41.4).

EXTERNAL MORPHOLOGY. The body is oval to elongate (Fig. 1A), with the posterior end of the foot covered by the mantle. The dorsum is covered with caryophyllidia about 100 μm long (Fig. 2D). The body is pale yellow to orange or brown. The dorsum is covered with a number of brown patches distributed regularly all over the surface. The rhinophoral sheaths are elevated and inflated. The rhinophores are dark brown with the apex white. The gill is composed of 12 unipinnate branchial leaves, which are yellow to dark brown. Near the edge of the mantle there is a row of opaque white mantle glands.

The anterior border of the foot is grooved and notched (Fig. 3B). The oral tentacles are short and triangular.

ANATOMY. The labial cuticle is smooth. The radular formula is $45 \times (50.0.50)$ in a 13 mm preserved length specimen (LACM 2003-41.4). Rachidian teeth are absent (Fig. 2A). The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 2B). The teeth increase in size gradually toward the medial portion of the half-row. The outermost teeth are also hamate and lacking denticles (Fig. 2C).

The reproductive system is triaulic (Fig. 3A). The ampulla is long and convoluted. It enters the female glands near their nidamental opening. The prostate is large and granular. It is divided into two different portions that are clearly distinguishable by their different texture and coloration. The deferent duct is long and expands into the muscular ejaculatory portion. The deferent duct opens into a common atrium with the vagina. There are no penial hooks. The vagina is long and narrow. At its proximal end, the vagina connects to the large and rounded bursa

copulatrix. Another duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about twice as large as the seminal receptacle (Fig. 3A).

GEOGRAPHIC RANGE. This species has been reported from Brazil (MacFarland, 1909; Marcus, 1955), Florida (Marcus and Marcus, 1967), South Carolina (Eyster, 1980), the Pacific coast Baja California (Bertsch *et al.*, 2000), southern Mexico (Ortea and Llera, 1981), and Costa Rica (Camacho-García and Valdés, 2003).

REMARKS. *Diaulula greeleyi* was originally described from Brazil (MacFarland, 1909) and was subsequently reported from several other Atlantic localities. Camacho-García and Valdés (2003) regarded the eastern Pacific species *Peltodoris nayarita* Ortea and Llera, 1981 as a synonym, based on the examination of specimens from the Pacific coast of Costa Rica. These authors also provided illustrations of the reproductive system and radula of this species based on Pacific material. The newly collected specimens from the Florida Keys are anatomically identical to the specimens from Costa Rica, confirming that the populations on both sides of the Isthmus of Panama belong to the same species.

Two other Caribbean species are *Discodoris mortenseni* Ev. Marcus and Er. Marcus, 1963, originally described from Curaçao and Tobago (Marcus and Marcus, 1963), and *Discodoris phoca* Ev. Marcus and Er. Marcus, 1967, originally described from Biscayne Key, Florida (Marcus and Marcus, 1967). The reproductive system of *Discodoris mortenseni* was subsequently described by Bertsch (1975). These two species have a pinkish or brownish dorsum with darker spots. Differences between these two species and *Diaulula greeleyi* include the presence of jaws with jaw elements and dorsal white spots in *Discodoris mortenseni* and *Discodoris phoca*. Additionally, the radular teeth of *Discodoris phoca* are more angular and the outermost teeth of *Discodoris mortenseni* have small denticles. According to Marcus and Marcus (1963, 1967), both *Discodoris mortenseni* and *Discodoris phoca* have caryophyllidia, and the latter also has the prostate divided into two portions. Thus, these two species should be removed from *Discodoris* Bergh, 1877, which includes species lacking caryophyllidia (Valdés, 2002). Valdés and Gosliner (2001) diagnosed *Diaulula* as lacking jaws, but the systematic position of species with jaws and caryophyllidia has not been investigated. Therefore the status of *Discodoris mortenseni* and *Discodoris phoca* remains uncertain until comprehensive phylogenies of caryophyllidia-bearing dorids at the species level become available.

Diaulula greeleyi differs from *D. sandiegensis*, the type species of the genus, by having a darker background color, lacking dorsal rings on the dorsum, having unipinnate branchial leaves, and having larger, more hooked-shaped and smooth outermost radular teeth. The anatomy and external

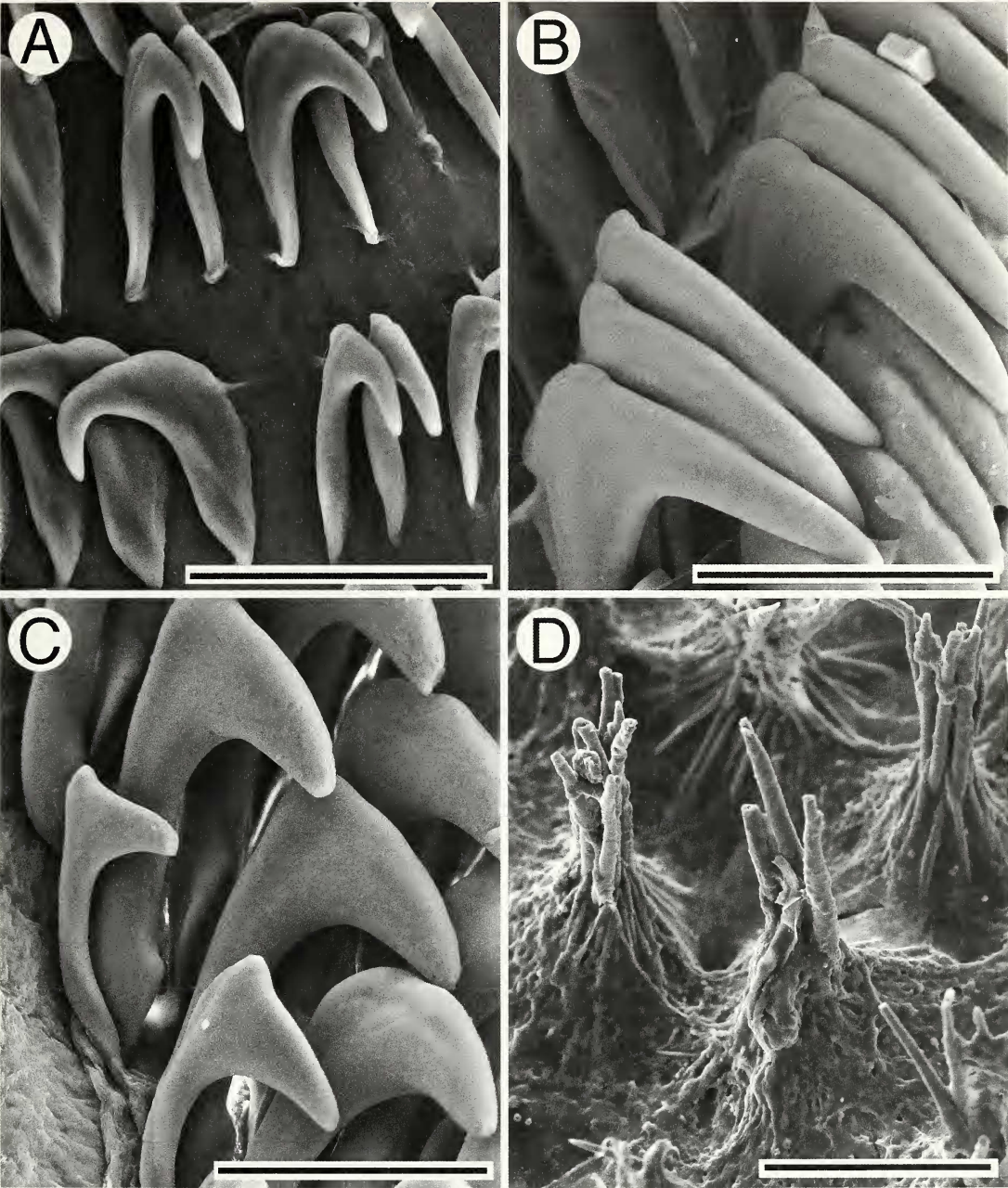


Figure 4 *Diaulula farmersi* n. sp., holotype (LACM 3016), scanning electron micrographs of radula and dorsum: A, Innermost lateral teeth, scale bar = 50 μ m. B, Midlateral teeth, scale bar = 50 μ m. C, Outermost lateral teeth, scale bar = 50 μ m. D, Caryophyllidia, scale bar = 100 μ m

morphology of *D. sandiegensis* was described in detail by Behrens and Valdés (2001).
The three other valid species of *Diaulula* found in the Americas are *D. punctuolata*, *D. hispida*, and *D. aurila* (see “Introduction” section). *Diaulula aurila* is also a tropical species redescribed by Camacho-García and Valdés (2003) and characterized by having a grayish background color with minute

brown and opaque white spots. The lateral profile of *D. aurila* is much lower than that of *D. greeleyi* and the radular teeth are more elongate and hamate. Both *D. punctuolata* and *D. hispida* are South American species that clearly differ from *D. greeleyi* in their external coloration. Illustrations of *D. punctuolata* and *D. hispida* by Schrödl (1996) reveal two lightly colored species, the former is pale

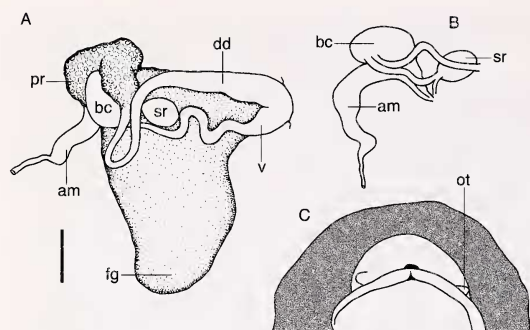


Figure 5 *Diaulula farmersi* n. sp., holotype (LACM 3016), anatomy: A, Reproductive system, scale bar = 1 mm. B, Detail of some reproductive organs, scale bar like in A. C, Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am = ampulla; bc = bursa copulatrix; dd = deferent duct; fg = female glands; ot = oral tentacle; pr = prostate; sr = seminal receptacle; v = vagina

creamish-white with light brown spots and the latter is completely white, and both have tripinnate branchial leaves.

There are no other species of dorid nudibranchs from the Atlantic or other biogeographic regions assigned with certainty to the genus *Diaulula* (see "Introduction" section).

Diaulula farmersi new species

Figs. 1B, 4–5

TYPE MATERIAL. Holotype. Shore in front of the Bayside Resort (mile marker 99.5), Key Largo, Monroe County, Florida, 13 July 2003, 1–2 m depth, 9 mm preserved length, leg. A. Valdés (LACM 3016).

EXTERNAL MORPHOLOGY. The body is oval to elongate (Fig. 1B), with the posterior end of the foot covered by the mantle. The dorsum is covered with caryophyllidia, about 150 μ m long (Fig. 4D). The body is yellowish gray and has a number of minute brown dots all over the surface. The rhinophoral sheaths are elevated and inflated. The rhinophores are dark brown with the apices white. The gill is composed of 9 bipinnate branchial leaves, which are uniformly white. Near the edge of the mantle there are 2 rows of opaque white mantle glands. The outermost row is composed of small glands densely packed, the innermost row has a few larger and irregular glands.

The anterior border of the foot is grooved and notched (Fig. 5C). The oral tentacles are short and triangular.

ANATOMY. The labial cuticle is smooth. The radular formula is $46 \times (50.0.50)$ in the holotype (LACM 3016). Rachidian teeth are absent (Fig. 4A). The lateral teeth are hamate, having a single cusp and lacking denticles (Fig. 4B). The teeth increase in size gradually toward the medial portion

of the half-row. The outermost teeth are also hamate and lacking denticles (Fig. 4C).

The reproductive system is triaualic (Fig. 5A). The ampulla is long and curved; it enters the female glands near their nidamental opening. The prostate is large and granular; it is divided into two different portions that are clearly distinguishable by their different texture and coloration. The deferent duct is long and expands into the muscular ejaculatory portion. The deferent duct opens into a common atrium with the vagina. There are no penial hooks. The vagina is long and narrow. At its proximal end, the vagina connects to the large and oval bursa copulatrix. Another duct, which connects to the seminal receptacle and the uterine duct, leads from the bursa copulatrix. The bursa copulatrix is about three times as large as the seminal receptacle (Fig. 5B).

GEOGRAPHIC RANGE. This species is only known from the type locality in the Florida Keys.

ETYMOLOGY. Dedicated to Farmers Insurance Group for their generous contribution to the education and research programs of the Natural History Museum of Los Angeles County.

REMARKS. A review of the literature revealed that there are no other species similar to *Diaulula farmersi* in the tropical western Atlantic. The most similar species in external morphology and coloration is an unnamed animal from Cape Verde, West Africa, illustrated by Ortea (1998:pl. 1A), which differs from *D. farmersi* only in the yellowish color of the gill. Ortea (1998) introduced the name *Doris hayeki* based on two uniformly yellow animals also collected from Cape Verde. The photos of the living animals show that they clearly belong to two different species. One of them (from Boavista) has the dorsum covered with caryophyllidia (Ortea, 1998:pl. 1A), whereas the other (from Sal) has simple, rounded dorsal tubercles (Ortea, 1998:pl. 1B). Ortea (1998) designated as the holotype the specimen from Sal, which is identical to the original description of *Doris atypica* Eliot, 1906. The generic placement and anatomy of the specimen from Boavista is unknown.

Diaulula farmersi is clearly distinguishable from *D. greeleyi* by the external coloration, which is uniformly yellowish gray with minute brown dots and white branchial leaves in the former and pale yellow to orange or brown with brown patches and yellow to dark brown branchial leaves in the latter. Anatomical differences include the size of the bursa copulatrix and prostate, which are proportionally smaller than in *D. greeleyi*. Examination of Panamic specimens of *D. greeleyi* by Camacho-García and Valdés (2003) revealed that the external coloration and anatomy of their specimens is virtually identical to that of the Atlantic specimens here studied. Additionally, very little variability has been observed among specimens of different sizes collected from the Florida Keys. It is clear that *D. greeleyi* has a very conservative anatomy and external coloration; thus, differences with *D. farmersi* are

not due to intraspecific variability or state of maturity.

Differences between *Diaulula farmersi* and *D. sandiegensis* include the presence of dorsal rings on the dorsum and tripinnate branchial leaves in the latter. Also, *D. punctulata* and *D. hispida* are much lighter species, having tripinnate branchial leaves.

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